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Studies on the Structure of Japanese Species of *Ranunculus*

Contributions to Cytology and Genetics from the Departments of Plant-Morphology
and Genetics, Botanical Institute, Faculty of Science,
Tokyo Imperial University, No. 88

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With 2 Plates and 18 Text-Figures

Contents

| | |
|--|-----|
| I. Introductory | 297 |
| II. Stem Habit and its Modifications | 299 |
| III. Course of Vascular System in the Stem and Rhizome | 302 |
| IV. Histology of the Stem and Rhizome | 310 |
| V. Course of Vascular System in the Floral Organs | 317 |
| VI. Histology of the Floral Organs | 321 |
| VII. Structure of the Root | 323 |
| VIII. Tuber of <i>Ranunculus Zuccarini</i> MIQ. | 325 |
| IX. Leaf of <i>Ranunculus flagellifolius</i> NAKAI | 330 |
| X. Relationship among the Species Studied | 333 |
| XI. Summary | 335 |
| XII. Literature | 339 |
| XIII. Explanation of the Plates | 342 |

I. INTRODUCTORY

Our present knowledge regarding the structure of the Ranunculaceous forms is mostly due to the authors of the Liège school such as LENFANT, MANSION, STERCKX, LONAY, GOFFART and NIHOUL. Besides the members of the Liège school, numerous authors have studied the structure of the chief representatives of the family from various points

of view. In his classic work, MARIE (1884, p. 168) expressed the opinion that the genus *Ranunculus* is the most typical one from which other forms of this family may be derived, and JEFFREY (1899) studied the ontogeny of the central cylinder of that genus in establishment of his stelar theory.

Ranunculus is the largest genus in Ranunculaceae and some species are submerse plants while others are land ones with erect or creeping stems, and there is some room yet for accurate study and description of the structure of those forms, particularly in respect to the vascular course and histology both in the floral and vegetative organs and moreover to the relationship between each species.

In the present study of *Ranunculus*, the structure of the following 16 species was examined by the writer, namely :

Ranunculus Vernyi FRANCH. et SAV. var. *japonicus* NAKAI

R. chinensis BUNGE

R. Tachiroi FRANCH. et SAV.

R. acris L. var. *Steveni* REGEL

R. japonicus THUNB.

R. sceleratus L.

R. Zuccarini MIQ.

R. yatsugataensis HONDA et KUMAZAWA

R. pygmaeus WAHL.

R. altaicus L. var. *minor* NAKAI

R. Kawakamii MAKINO

R. flagellifolius NAKAI

R. aquatilis L. var. *flaccidus* MAXIM.

R. nipponicus NAKAI

R. yaegataensis MASAMUNE

R. yakushimensis MASAMUNE

All of these species, except the last two which are found in Yakushima, occur in Hondo, some being distributed widely in Japan, while others are in rather limited region.

R. acris, *R. sceleratus*, *R. pygmaeus* and *R. aquatilis* are found also in Europe, so that some anatomical notes on these species have been already given by some authors.

Most species of *Ranunculus* cited above belong to the subgenus '*Euranunculus*' of PARKIN (1928) and his other subgenus '*Leucoranunculus*' is represented only by two submerse species, *R. aquatilis* and *R. nipponicus*.

In the present investigation, successive sections are made by the

usual paraffin method in the case of the delicate materials such as the seedling, the floral and vegetative organs, but in order to understand both the behaviour of the vascular strands in the stem and rhizome and the relation between leaf traces and stem bundles, the following method was devised by the writer in the case of the vigorous species.

The materials which are sometimes 20 cm. or more in length are immersed in 3—10 % NaOH or KOH for a few days or more, or are boiled in a 3 % solution for a few minutes to soften the tissue but not long enough for it to be macerated. With the best management by the solution just described, the cortex and epidermis of the material are found to be softened, but the fibrovascular strands remain comparatively more stable. After washing half an hour in water and then immersing in slightly acidulated glycerine-alcohol, both epidermal and cortical tissues of the materials, which are now semitransparent, are macerated by means of the needles so as to trace the course or distribution of the vascular system under the demonstration-microscope. If phlorogrucinol and hydrochloric acid are used, even the most complex vascular course may be easily traced.

It is rather difficult to determine the vascular course or distribution through many internodes, which are pretty long, by the reconstruction of the cross sections, although this method was introduced by NÄGELI (1858) and adopted by various authors for their studies of the vascular course in the phanerogamic stem. By the method cited above, the writer was able to trace the bundle course of some vigorous stems of *Ranunculus*, which may attain about half a meter in length, but the method can not be applied, of course, to the delicate species and materials.

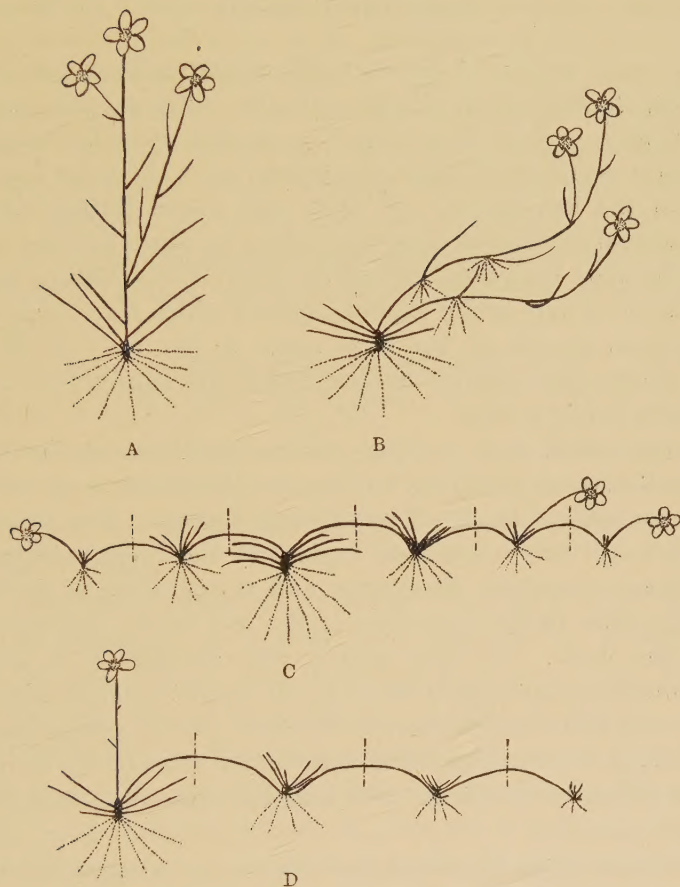
II. STEM HABIT AND ITS MODIFICATIONS

All the species, belonging to the section *Batrachium* including *R. aquatilis* and *R. nipponicus*, are submerse plants, having elongated slender internodes and usually filiform submerse leaves. In some parts of the stem, several successive internodes are practically shortened, being 1—3 mm. in length, and a few adventitious roots which occur at each node, are long and filiform usually without lateral rootlets. These roots may or may not fix in the soil, but such a part as rhizome of other land forms does not differentiate in these aquatic species and all the parts of the stem do not, as a rule, wither away even in the winter. This fact is mostly due to the adaptation to the aquatic habit of the species, for in

the case of the most land forms of *Ranunculus* the aerial parts of the plant disappear usually in the winter, therefore some geophilous reserve organs must differentiate if the plant is neither annual nor biennial.

The land forms of *Ranunculus* studied, grow on rather wet ground, some of them e. g., *R. sceleratus*, *R. Vernyi*, *R. Kawakamii*, *R. flagellifolius*, are found even in marshy soil. Among Ranunculaceae, though such a tendency is usually found also in *Cimicifuga* and *Caltha*, this is not a prevalent habit in this family; whether it is a derived one or not is left undecided.

Most species have erect stems and their terminal ends are occupied always by the peduncles (Text-fig. 1, A). Some vigorous stems of *R. sceleratus* reach .3 cm. or more in diameter at a basal cross section, and lateral shoots occur on each node of the aerial stem and also on the upper parts of the rhizome. In the slender species such as *R. pygmaeus*, *R. altaicus* and *R. yatsugatazensis*, the erect stem, the diameter being usually 3 mm., has only a few nodes and no lateral shoot is observed. On the other hand, some species such as *R. flagellifolius* produce a few numbers of the creeping stems (stolons) from a rhizome in spring (Text-fig. 1, C). A stolon of *R. flagellifolius* is filiform, its diameter being 2 mm., and has usually three or four nodes from which adventitious roots appear for the purpose of absorption. The first leaf of the stolon node, being a few millimetres in length, is reduced into the scaly form, but other ones, belonging to a shortened lateral shoot at the node, are always normal in their shape. Peduncles occupy the terminal end of the creeping stem. After the stolon adventitious roots penetrate into the ground far enough to absorb water, the original connection between each node of the stolon is destroyed by decay of the internodal regions, thus an individual plantlet results from each stolon node respectively. In several examples the stems of some species e. g., *R. Vernyi* var. *prostratus* NAKAI, show adventitiously or habitually the creeping habit, producing adventitious roots from the nodal regions (Text-fig. 1, B); in these cases it is not observed that each node becomes an individual plantlet by decay of the internodal parts. From this respect the two modifications of the aerial stem of *Ranunculus* are clearly distinguished, but it is interesting to note that in *R. Kawakamii* the stolons, whose terminal produces no flowers, grow apparently as in the case of *R. flagellifolius*, but besides stolons, an erect stem with a few nodes occurs from the same plant, which terminates with flowers (Text-fig. 1, D). In this example the two modifications of the stem habit occur normally in one and the same plant.



Text-fig. 1. Diagrams showing the stem habit of the land forms. Explanation in text.

It seems probable to the writer that among the land forms of *Ranunculus* the original type of the stem habit is the erect one, as found in *R. aris*, *R. Vernyi*, *R. sceleratus*, *R. Zuccarini*, *R. chinensis*, etc., and the most derived one is represented by *R. flagellifolius* which has creeping stems only. *R. Kawakamii* shows the transitional modification of these two types, having both erect and creeping stems. The case of *R. Vernyi* var. *prostratus* is a rather modified one from the first type.

III. COURSE OF VASCULAR SYSTEM IN THE STEM AND RHIZOME

In a cross section of the internode of the vigorous species such as *R. Tachiroi*, *R. chinensis*, *R. Vernyi*, etc., the fibrovascular strands are arranged more or less in a ring, the smaller strands, being situated rather more peripherally than the greater ones, the latter having close relation to the leaf traces. If they are traced farther downwards through several internodes, they diminish in size, immigrating gradually towards the more peripheral part of the stem. This feature is demonstrated more clearly in the vigorous species which have large numbers of the vascular strands in the stem, than in the case of the slender species, whose stem bundles and leaf traces are reduced in number and are of rather uniform size.

In this genus, the vascular courses have scarcely been studied except in *R. arvensis* described by NIHOUL (1890)¹⁾ and in *R. bulbosus*, *R. montanus* and others described by ZIEGLER (1895).¹⁾ The latter author studied however only a few nodal regions by the cross section without tracing many successive internodes and nodes, thus he showed some different features in the behaviour of the leaf traces between the two species cited above. But their results seem insufficient to understand the general characteristics of the vascular course of *Ranunculus*.

The writer studied ten species including both vigorous and slender forms through several internodes of the aerial stem by his own method, or by the reconstruction from cross sections as usually adopted by other authors.

The forms with big stems have numerous vascular bundles sometimes reaching 60 strands in number in a cross section of the internode, but in the slender forms usually only three to four are observed (Table I). The strands of the stem run down without connecting with each other in the internodal parts, but the bundle courses in the nodal region are, in most cases, too irregular to be easily understood, owing to the occurrence of the lateral shoots and of the nodal complexity or the lack of uniformity in the features of the vascular course itself. Generally speaking, in the typical case, some strands which come down from the upper internodes, divide into two at the node, and each of them fuses

1) There are some differences of vascular topographies between their descriptions and the result of the present writer, but they may be due to the difference of the method adopted.

with the neighbouring stem strands on both sides; between the divided two strands mentioned above, a strand of a leaf trace comes from the petiole, running downwards and some of such leaf trace strands fuse to the stem strands at the lower node, sometimes at the next node, but usually at the third or fourth node.

Further study shows that there are two types of leaf trace strands which may usually be recognized; the one (Type A) goes down at least to the next internode almost without fusing with any stem strand, though it may or may not be connected laterally by small bundles at the first node or at its neighbourhood; while the other (Type B) attaches immediately to the stem bundles without going down as in the case of the former type.

Conveniently to demonstrate the behaviour of the strands, capital letters M and L were used in this paper²⁾ to denote the leaf trace strands of the type A, small letters m and l those of the type B, and nL or nl to denote some numbers of L or of l which may easily disappear or may change their characteristic tendencies of the two types in the stem of the same species.

The leaf trace strands of the type A belonging to a leaf, are usually constant in number in each node; for example in *R. Vernyi* (Plate I, Fig. 2), *R. acris* (Plate I, Fig. 6), *R. sceleratus* (Plate I, Fig. 1), they are always three (L_1 , M, L_2); in *R. Kawakamii* (Plate I, Fig. 7), *R. flagellifolius* (Plate I, Fig. 9), *R. pygmaeus* (Plate I, Fig. 5), *R. Zuccarini* (Plate I, Fig. 4) and *R. aquatilis* (Plate I, Fig. 8) only midrib (M) is of type A; while in *R. chinensis* (Plate I, Fig. 3) and *R. Tachiroi*, the leaf trace strands of the type A are variable in number, being more than three in each node (nL_1 , L_1 , M, L_2 , nL_2), and at a lower node about ten strands of this type are observed, although most of them are reduced into three (L_1 , M, L_2) at the lower node. The number of the leaf trace strands of the type B is always two (l_1 , l_2) in the species which have only one strand (M) of the type A as shown in *R. Kawakamii*, *R. flagellifolius*, etc., while they are variable in the species which have three or more leaf trace strands of the type A in each node.

The exact number of the strands is given in the Table I.

2) In his study of the Ranunculaceous leaves, GOFFART (1901) used also the letters M, L and m in order to denote each of the petiolar strands, without taking notice of the nodal condition of the leaf trace strands.

TABLE I

| <i>Ranunculus</i> | Stem diameter at the basal cross section. mm. | Number of the stem bundles at the basal cross section | Number of the vascular strands at the lowest part of a petiole | Number of the leaf trace strands of the type A in a node | Number of the leaf trace strands of the type B in a node | Type of the leaf trace in a node |
|---|---|---|--|--|--|--|
| <i>R. chinensis</i> | 10-15 | 25-70 | 3-5-15 | 3-9 | 2-6 | $nL_1 L_1 M L_2 nL_2$ $l_1 l_1 M L_2 l_2$ |
| <i>R. Tachiroi</i> | 7-13 | 39-51 | 3-5-13 | 3-8 | 2-5 | " |
| <i>R. Vernyi</i> | 10-15 | 20-50 | 3-5-15 | 3 | 2-10 | $n l_1 L_1 m_1 M m_2 L_2 n l_2$ |
| <i>R. acris</i> <i>R. japonicus</i> ** | 5-6 | 13-27 | 3-9 | 3 | 2-6 | " |
| <i>R. sceleratus</i> | 10-15 | 17-30 | 3-6 * | 3 | 0-3 | $l_1 L_1 m_1 M m_2 L_2 l_2$ |
| <i>R. Zuccarini</i> | 3 | 6-9 | 3 | 1 | 2 | $l_1 M l_2$ |
| <i>R. pygmaeus</i> | 1.5 | 4-5 | 3 | 1 | 2 | " |
| <i>R. Kawakamii</i> | 3 | 3-6 | 3 | 1 | 2 | " |
| <i>R. flagellifolius</i> | 2-3 | 3-8 | 3 | 1 | 2 | " |
| <i>R. altaicus</i> | 3-4 | 7-12 | 3 | 1 | 2 | " |
| <i>R. yatsugataensis</i> | 3 | 7-14 | 3 | 1 | 2 | " |
| <i>R. aquatilis</i> <i>R. nipponicus</i> | 3 | 3-6 | 3-5 * | 1 | 2-4 | $l_1 m_1 M m_2 l_2$ |

*NESTLER (1894, p. 299) and GOFFART (1900, p. 104) described that a petiole is supplied with three vascular strands in this species, but four to six strands were often found in our materials.

**According to Professor T. NAKAI, the taxonomic differences between the two species have not yet accurately been established.

To understand the feature of the leaf traces more accurately, comparative study of the seedlings was made. NIHOUL (1871), described the feature of the seedling vascular course of *R. arvensis*³⁾ in detail, and BLACKBURN (1917) studied the epicotylar structure of the genus, dividing the genus into four different groups; most of them, except one group to which *R. arvensis* belongs, deviate from the normal vascular type of other Ranunculaceae seedlings.

Among the several species studied by the present writer, two modifications of the seedling central cylinder are clearly demonstrated; namely young leaves of the seedling of *R. Vernyi*, *R. acris*, *R. chinensis* and *R. aquatilis* have three leaf trace strands, each of which cause a leaf gap of its own upon the central cylinder, while in *R. Zuccarini* (Text-fig. 4, A) three leaf trace strands, belonging to a young leaf, occur usually from a common gap. The former case is prevalent in *Ranunculus* seedlings and Text-fig. 2 shows the seedling central cylinder of *R. Vernyi*, an example of this type. In this case each of the first to fourth leaves is supplied with three strands, but at the fifth node, five leaf trace strands are recognizable, two of them being small in size and bending almost immediately outwards from the central cylinder. These small ones (m, l)



Text-fig. 2. Diagram showing the seedling central cylinder of *R. Vernyi*, reconstructed from the cross sections. One of the lateral strands at the first node occurs abnormally from a cotyledonar gap. At the sixth node only the midrib is shown. *c*₁, *c*₂, cotyledonar traces. × denotes the points of exit of the early adventitious roots.

3) In the diagram shown by NIHOUL (1891, Pl. III, Fig. 32), the vascular topography of the species is not similar to any example studied by the present writer. According to him, the gaps of the central cylinder caused by the exit of the leaf trace, are not closed again in the case of the seedling of *R. arvensis*.

correspond to the leaf trace strands of the type B in the adult stem, being variable in number. The strands of the type A develop quite clearly from the first foliar node and are always three in number in each node throughout the stem. The seedling central cylinder of *R. chinensis* is quite the same with that of *R. Vernyi* as to the foliar supply, but at the upper nodes the strands of the type A increase more than three in number. The seedling internode of the submerse species is



Text-fig. 3. Diagram showing the seedling central cylinder of *R. aquatilis*. The first leaf has not both lateral nerves, the second one has only one of them. The midrib is connected by the small lateral strands at each node. *c*₁, *c*₂, cotyledonary traces.

much longer than that of the land forms. Then the seedling central cylinder of *R. aquatilis* was examined and shown in Text-fig. 3. In this species, three leaf trace strands occur also from three separate gaps respectively, only midrib M corresponding to the strand of the type A in the adult condition (compare Plate I, Fig. 8), but it is worthy of note that the midrib is connected laterally by the small strands at each node and such a feature is also found in the central cylinder of the seedling as well as in that of the adult.

Text-fig. 4, A shows the very young seedling central cylinder of *R. Zuccarini* which represents the other modification. There are three strands which belong to a leaf and occur, as a rule, from a common leaf gap (unilacunar condition according to the terminology of SINNOTT), and the middle strand M occurs from the base of the gap, while the lateral two, being small in size, occur from the lateral parts of the same gap, or from the neighbourhood of the gap. The former strand is of the type A and the latter, of the type B corresponding to those of the adult stem; but at the later stage of the seedling, three strands, belonging to a leaf, do not apparently pass out from the margin of a common gap but from the separate gaps respectively as shown in Text-fig. 4, B. This may be probably due to the new appearance of the gaps and also to the dislocation of the leaf trace strands from one gap to another, and it is of significance for those suggestions that the lateral nerves in Text-fig. 4, A may not sometimes



Text-fig. 4. Diagrams showing the central cylinder of *R. Zuccarini*.

A: Very young seedling. The leaf trace strands belonging to a leaf occur from the margin of a common gap or its neighbourhood. One of the lateral strands at the first foliar node does not develop. The leaf traces at the third node do not yet differentiate except the midrib M_3 . c_1 , c_2 , cotyledonar traces. X denotes the points of exit of the first and second tubers.

B: More developed seedling than A. Three leaf trace strands belonging to a leaf do not now occur from a common gap. b , vascular bundles to the axillary buds. Cotyledonar node is not shown.

occur exactly from the margin of the gap of the midrib, but from a point on the central cylinder a little separated from the margin of the gap.

In this respect more exact study is now in progress, but as diagrammed in the Text-fig. 5, if two lateral strands of the leaf trace of unilacunar condition (Text-fig. 5, A; l_1, l_2) elongate a little more upwards joining with the stem strands, then unilacunar condition of the leaf trace becomes trilacunar (Text-fig. 5, B).

In fact, such an example of the dislocation of the leaf trace strands⁴⁾ seems to be manifested in the central cylinder of the rhizome and stem of *Ranunculus* (Text-fig. 4, B; Plate I, Fig. 4, Fig. 8), therefore



Text-fig. 5. Diagrams showing the behaviour of the leaf trace strands at a node.

A: Unilacunar condition of the node.

B: Its modification caused by the elongation of the two lateral strands l_1 and l_2 , thus the unilacunar condition of the node changing itself into the trilacunar condition.

some interpretations regarding the leaf gap must be carefully considered, for the apparent gaps of the central cylinder of this plant group are extraordinarily difficult to be identified as original leaf gaps, if the dislocation of the leaf trace strands is accepted. Then it is worthy of note that in a node of the herbaceous plant, at least in that of *Ranunculus*, the number of the leaf trace strands of the type A seems to the

writer to be much more important than the number of the leaf gaps observed in a cross section of the node, although SINNOTT (1914) deduced an interesting phylogenetic conclusion from the number of the leaf gaps at the angiospermal node.

In short, the typical leaf trace found in *Ranunculus* consists of three strands (L_1, M, L_2), each of which causes a gap of its own and runs downwards from the node through some internodes, without connecting immediately with the stem bundles, but on the other hand the feature of the vascular course of the stem may diverge by both amplification and reduction of the leaf trace strands and of stem strands. This divergence is probably due to the adaptative tendency; for *R. sceleratus* and *R. Zuccarini*, for example, differ in the type of their vascular be-

4) After this study was made, the writer had an opportunity to know that this 'Dislocation Theory' of the leaf trace strand was also suggested quite independently by Professor B. HAYATA in the case of the rhizomes of other families of Dicotyledons.

haviour, although both species are included in the same section *Epirotes* taxonomically and are rather closely related with each other histologically. The complexity of both vascular course and nodal condition occurs chiefly in the vigorous species and the reduction may be recognized in the slender species of this genus. When a leaf trace comes to reduction, the strands of the type A change their behaviour into the type B, combining with the stem bundles rather immediately at the point of the foliar exit and reducing their size; in the second stage thus induced strands of the type B may easily disappear.

The rhizome of *Ranunculus* is usually erect, covered all around with numerous adventitious roots, and it is very short and of a cannon-ball shape, 2 cm. in length in the biggest example of the vigorous species, while the rhizome of some species such as *R. altaicus*, *R. pygmaeus*, *R. auricomus*, etc., elongates rather obliquely into the ground, being somewhat long and slender.

The vascular distribution in the rhizome presents an aspect of the network in surface view. In the young rhizome of *R. Vernyi*, the strands which anastomose with one another are rather slender, leaf traces being visible in each wide mesh of the vascular skeleton, but in the full-grown rhizome of the older stage the network of the bundles tangles more densely, for the meshes of the net are somewhat reduced in area by the secondary thickening of the vascular strands, thus only small leaf gaps are observed on all sides of the vascular skeleton. Therefore, as seen in the cross section, the vascular cylinder is disturbed only at the several points by the narrow leaf gaps. Corresponding to the secondary thickening of the rhizomal bundles, the mesh of the vascular net tends to be further eliminated until the original leaf gaps are greatly obscured as found in the extreme case of *R. chinensis*. On the contrary, the full-grown vigorous rhizome of *R. sceleratus* has netted vascular topography scarcely presenting any reduction of the leaf gaps throughout its life, although the strands themselves become more or less thickened at the later stage. *R. Zuccarini* has the rhizomal vascular network of the same texture but of a smaller scale.

Two types of the leaf trace strands are rather difficult to identify, for the internodal elongation is greatly reduced in this organ.

IV. HISTOLOGY OF THE STEM AND RHIZOME

A. THE STEM

One of the most characteristic features of this genus is the occurrence of the bundle sheath⁵⁾ which, in extreme case, develops and completely encloses each bundle of the aerial stem. Such a feature is not common in dicotyledonous species as already known, but is found very often in Monocotyledons, in which, however, the bundles are scattered in the fundamental tissue and the secondary growth is entirely reduced. In the full-grown stems of *R. Vernyi*, *R. Tachiroi*, *R. chinensis*, *R. acris*, *R. japonicus*, *R. yakushimensis*, etc., the thick-walled cells of the bundle sheath, which completely encloses each bundle respectively, are derived ontogenetically from the parenchymatous layers such as endodermis, pericycle and the parenchyma on both sides of these layers.

The mode of the development of the bundle sheath will be described in an example of *R. Vernyi*.

A little after the lignification of the Casparian strips of the endodermis which is of an individual type in the aerial stem, the cell walls of the pericycle and of the endodermis and also those of a row of the parenchymatous cells which touch to the pericycle, begin to be slightly lignified on the xylem side and then on the phloem side or vice versa, so as to form the fibrous arcs. The lignification of both arcs goes on further until the thickness of the membranes increases enough to form the protecting sheath, although two arcs do not connect to form a ring. But the bundle sheath, found in the full-grown stem, forms a fibrous ring which fully encloses the bundle (Plate II, Fig. 10; *R. acris*). At this stage the sheath consists of about four to six layers of the lignified cells which have now rather small spaces respectively, but only a few layers of the unchanged parenchymatous cells are observed between the inner layer of the sheath and the group of the vessels. Therefore the original position of the endodermis and the pericycle, which are recognizable at an early stage, can be no

5) The mechanical fibrous tissues of the Ranunculaceous forms were considered as the most important characteristic feature by SCHWENDENER, MEYER, NESTLER, HIMMELBAUR, etc. MEYER (1884, p. 28) described in *Ranunculus*: "Zwei anatomische Merkmale spielen bei der Characterisierung der Ranunculus-Species eine Hauptrolle: Der vorher schon so vielfach erwähnte Festigungsring und die hier im Verein mit ihm auftretende, sich um die Gefäßtheile der Bündel herumziehende Strangscheide, die bei den Land-species verdickt und verholzt, bei den Wasserspecies aber nur angedeutet ist." 'Festigungsring' means the interfascicular fibrous cylinder in this paper.

longer distinguished from other lignified elements of the sheath. This extraordinarily developed bundle sheath, found often in the vigorous stem of *Ranunculus*, is one of the monocotyledonous features so generally well known.

Various stages of the development of the sheath are easily found even in the different levels of one and the same stem.

In the vigorous species, the bundles with these bundle sheaths are usually connected by an interfascicular fibrous cylinder with each another, but it seems to the writer that this fibrous cylinder is of less significance to be described than the bundle sheath itself.

In some species the bundle sheath does not enclose each bundle entirely, but is presented by two different fibrous arcs consisting of a few layers of the lignified cells on both the xylem and phloem sides, or only by one arc sheath on the phloem side, even in the most fully grown stem. In the submerse species such as *R. aquatilis* and *R. nipponicus*, a very reduced bundle sheath which consists usually of one or two layers of the slightly lignified elements, may or may not be recognizable in the nodal region of the old stem.⁶⁾ Generally speaking, among the water plants, it is usual that the lignification of the cell walls is extraordinarily reduced in both mechanical and conducting elements. In the aquatic *Ranunculus*-species cited above, the lignification of the vessels is very weak if it does occur, while that of the reduced bundle sheath is found to be more advanced. This fact induces the writer to suggest that the formation of the bundle sheath may be due to both phyletic and adaptative tendencies but not merely to the adaptative tendency among this genus, and the writer proposes to call the bundle with the sheath which encloses each bundle all around, forming a fibrous ring, as the 'Ranunculus Type,' one of the most characteristic vascular types among *Ranunculus* (Plate II, Fig. 10: *R. acris*). On the other hand, in the stem bundles of some species such as *R. sceleratus*, *R. Zuccarini*, etc. (Plate II, Fig. 11: *R. sceleratus*), the perfect bundle sheath does not develop, the bundles being protected by the fibrous mass only on the phloem side, and both lateral arms of the mass do not elongate to surround each vascular bundle even in the full-grown condition of the stem. On the xylem side a distinct sheath does not occur, though the walls of some parenchymatous cells may be lignified slightly without thickening of the walls. In the bundle of the

6) But MEYER (1884, p. 29) and SOLEREDER (1899, p. 22) described that the section *Batrachium* has no mechanical tissue in the stem bundle. On other hand, NESTLER (1894, p. 300) recognized the sclerenchymatous cells on the xylem side in the petiole of *R. aquatilis*.

former type, the secondary growth is greatly interrupted by the closed mechanical sheath, but in that of the latter type, as the bundle is free from the closed sheath, some amounts of the secondary elements may possibly occur as in *Clematis* among Ranunculaceae. In the bundle of *Anemone*, which the writer is now studying, the occurrence of the bundle sheath such as found in *R. sceleratus* is most prevalent, though the secondary xylem elements are lacking in that bundle. Therefore the writer names the latter type of the bundle as the 'Anemone Type' for convenience, although it is not only a characteristic of the bundle of *Anemone* but also of almost all the genera of this family.

It must be noted that the two types are not, of course, clearly distinguished particularly in the immatured plants, and also that in the case of the full-grown ones, *Ranunculus* type occurs in one organ, but may not in other organs.⁷⁾ Nevertheless the case is not found in which the bundle of the stem is of the Anemone type while that of the petiole in the same plant is of the *Ranunculus* type among any species of *Ranunculus*, although such an example was described in *Helleborus* by NESTLER (1893).

Even in the species which have the stem bundles of the *Ranunculus* type, this type is not recognizable in the bundles of the conservative organs such as the peduncle, floral receptacle and rhizome as will be touched upon in the later connection. Judging from this respect and from the fact that the *Ranunculus* type is rather prevalent among the monocotyledonous bundles without cambium, the *Ranunculus* type of the bundles seems to the writer to be more derived one than the other type i.e. the Anemone type in this genus, although this may not be accepted in the case of other genera.

In the full-grown stems of the species studied by the writer, the two types are found as shown in the following table :

TABLE II

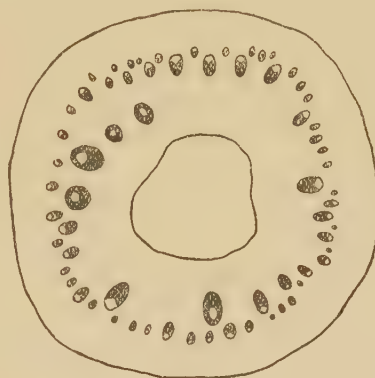
| Ranunculus Type | Anemone Type |
|---|---|
| <i>R. Vernyi</i> <i>R. Tachiroi</i> <i>R. chinensis</i> <i>R. japonicus</i> <i>R. acris</i> <i>R. yakushimensis</i> <i>R. yaegataensis</i> <i>R. flagellifolius</i> <i>R. aquatilis</i> <i>R. nipponicus</i> | <i>R. sceleratus</i> <i>R. Zuccarini</i> <i>R. altaicus</i> |

7) In the monocotyledonous stem of some species, both types of the fibrous sheath may be equally found in one and the same cross section. See SCHWENDENER (1874).

R. Kawakamii, *R. pygmaeus* and *R. yatsugatazensis* are considered to present the transitional form of both types even in the full-grown stem, for in those species a bundle arc occurs clearly on the phloem side and both arms of the arc elongate to the lateral sides of the xylem but never completely enclose the bundle.

Hitherto amphivasal concentric medullary bundles have never been described in this genus, but they were found by the writer abnormally occurring in the aerial stems of *R. chinensis* (Text-fig. 6) and *R. Vernyi*. In those species the leaf trace strands and stem strands are rather large in number (see Table I) and the amphivasal concentric bundles seem to correlate usually with the leaf traces, so that the hypothesis of JEFFREY (1926, p. 412) on the origin of the amphivasal concentric bundle may be accepted also in these cases.

Sometimes in *R. chinensis* a mass of the fibrous cells, derived from the bundle sheath, is enclosed within the centre of the phloem. The occurrence of such a feature was studied by NESTLER (1892, Tab. XXVI, Figs. 5-8) in detail in the case of the petiole of *Cimicifuga foetida* and the present example is similar to his description.



Text-fig. 6. Cross section of the stem of *R. chinensis*, showing the amphivasal concentric medullary bundles. Black area in the figure represents the xylem.

Mechanical tissues such as bundle sheath and interfascicular fibrous cylinder are not shown. ($\times 7$)

One of the most important characteristics of Ranunculaceae is the shape of the xylem which may be represented by the letter V. This is another interesting feature similar to the monocotyledonous plants, being never found, as a rule, among the dicotyledonous ones with exception of this family and some other small groups.⁸⁾

Two reasons may be suggested of the xylem in assuming the V-shape:

1. The elements of the xylem are different in size according to their position. At the sharp point of the V, the protoxylem differentiates

8) DE BARY (1877); pp. 335-336.
MARIÉ (1884); pp. 162-163.
HABERLANDT (1924); p. 328.

VESQUE (1881); p. 22.
SOLEREDER (1899); pp. 17, 20.

at first, and then the elements of the metaxylem develop, increasing their size towards both free arms of the V without containing almost any parenchymatous cell, but the smaller elements of rather uniform size are produced between the two arms of the V. Accordingly the xylem is usually concave in the direction of the protoxylem at the part between both lateral arms of the metaxylem, thus presenting the V-shape (Plate II, Fig. 10: *R. acris*). This shows that the V-shaped xylem is not due to the different activity of the cambial layer, and if the metaxylem consists of the elements of almost uniform size, the characteristic V-shape may disappear.⁹⁾

Such is the feature observed in the bundles of the stem of *R. altaicus*.

2. The degeneration of the cambial layer is one of the causes which produce the V-shape of the xylem. Among *Ranunculus* the secondary elements are greatly reduced in the stem bundle as already known¹⁰⁾, but they are fairly well produced in the conservative organs such as the floral receptacle, the peduncle and the rhizome. If we observe the bundle of these organs showing the secondary thickening, we may easily understand that the xylem consists of the elements of rather uniform size and assumes no more the V-shape as shown in Plate II; Fig. 13, Fig. 14 and Fig. 15. Also in an exceptionally large individual of *R. sceleratus* which reach 3.5 cm. in diameter at the basal part of the stem, great amounts of the secondary elements are produced to present the same aspect as described just above (Plate II, Fig. 11).

B. THE RHIZOME

The thickening of the rhizome is due to the secondary activity of the intrafascicular cambium and also to the cell division of the fundamental tissue, corresponding to the increase of the vascular bundles; and if observed in a cross section, the vascular strands may connect with one another laterally to form a vascular cylinder. In the older rhizome of *R. Vernyi* or of *R. chinensis*, the bundles with great amounts of the secondary elements are united with each other so closely that the gaps of the original leaf traces are much diminished in width. In the younger stage of those rhizomes, the bundles are separated by some amounts of the elements of the medullary rays from one another, but even in this case the characteristic features of the stem bundles such as the V-shaped xylem and well-developed fibrous bundle sheath are not recognizable.

9) MARIÉ (1884, p. 165) suggested this fact in the stem bundle of *Helleborus*.

10) MARIÉ (1884); p. 162. ANDERSON (1888); p. 17.

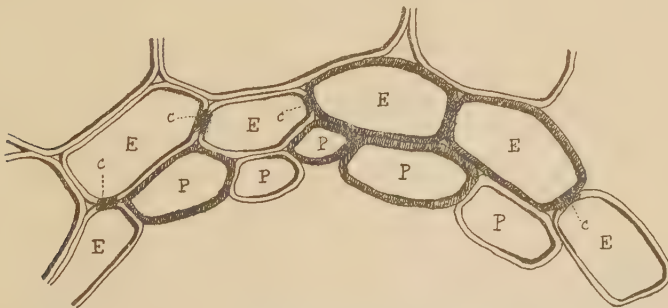
The central cylinder of rather elongated rhizome of *R. pygmaeus* may show sometimes the siphonostelic appearance without any foliar ray in a cross section.

The secondary elements of the xylem can be distinguished usually by their radial arrangement and their greater size and also by the small amounts of the xylem parenchyma.

C. ENDODERMIS

Concerning the endodermis of the stem bundles, MARIÉ (1884) described the individual type (astelic condition of VAN TIEGHEM) in *R. auricomus*, *R. flammula*, *R. hederaceus*, *R. peucedanifolius*, etc., while in the aerial stem of most species and even in the pedicel of *Hacatonia* (a section of *Ranunculus*) whose stem bundles have individual endodermis, the existence of the common endodermis was reported and these descriptions were cited afterwards by SCHOUTE (1903, p. 114), BLACKBURN (1917, p. 215) and probably by HABERLANDT (1924, p. 344).

In the present study, the stems of *R. Vernyi*, *R. acris*, *R. japonicus*, *R. Kawakamii*, *R. yakushimensis*, *R. yatsugataensis*, *R. scleratus*, *R. aquatilis*, *R. nipponicus* and probably *R. pygmaeus* and *R. yaegataensis* were ascertained to have the individual endodermis by the presence of the Casparian strips, although the development of the bundle sheath may obscure the endodermal position. Moreover, the endodermal position in some species is very hard to recognize, for the lignification of the Casparian strips does not occur generally in any stage of the stem bundles, but the careful study of the writer recognized, in a few cases, the slightly developed individual endodermis even in the species, such as *R. acris* and *R. scleratus*, which were described by MARIÉ as having the endodermis of the common type.



Text-fig. 7. Endodermal layer of the aerial stem of *R. acris* in rather early condition. Endodermal (E) and pericycle (P) cells are now thin walled. The reduced Casparian strips (c) appear on the radial walls of each endodermal cell, but soon they become obscure by the equal lignification of the walls. The dark parts show the lignified membrane. ($\times 600$)

Accurately tracing the endodermal differentiation of the stem in some species, e. g., *R. Vernyi*, both the lignification and the thickening of the Casparian strips may typically appear and soon the characteristic of the layer becomes obscure by the uniform thickening of the walls of the cells which compose the fibrous elements of the bundle sheath; but in other cases (Text-fig. 7), the radial walls of some endodermal cells, which surround each bundle, begin somewhat to be lignified, but the thickening of these radial walls or of a point on them does not occur, and then the lignification advances soon to all other sides of the walls uniformly and also to the walls of some other adjacent cell layers, thus the endodermal cells or layer becomes indistinguishable from the neighbourhood cells or layers. This is the case in the young plant of *R. acris*, but soon later, a very thick bundle sheath may be formed around each bundle.

More reduced endodermal development was observed in *R. sceleratus*, *R. Zuccarini*, *R. flagellifolius*, etc., in which the developmental and histological differences between the endodermal and other pericyclic or mechanical layers are scarcely recognizable by the loss of the Casparian strips or of the lignification on the radial walls; but on most careful observation in various parts of the stem, the cell walls of a layer may be recognized as lignified uniformly a little sooner than those of other cell layers, though not always.

Generally speaking, the endodermal layer shows, in the ordinary stems of *Ranunculus*, the reducing tendencies of the characteristic feature, being replaced by the well-developed bundle sheath or allied tissue; and in some species the endodermal layer may be observed, in rare cases, only in the young parts or periods of the erect stem or in the stem which adventitiously becomes subterranean, although it is clearly recognizable in all the parts and periods of the stem in other species.

In short, the writer could not, by any chance, have an opportunity of observing the endodermis of the common type even in the species described by MARIÉ as having such a type, or get any clue to it, although in some species the endodermal position of the individual type could not be ascertained in all probability.

It seems, therefore, to the writer most probable that the vascular bundles are always astelic in the aerial stems of *Ranunculus* and in the peduncles of the section *Hecatonia*¹¹⁾ and further that the endodermal

11) The structure of the following species which had been included in the section *Hecatonia*, were described by MARIÉ, namely: *R. aconitifolius*, *R. parnassifolius*, *R. amplexicaulis*, *R. Lingua*, *R. Flammula*, *R. cymbalariae*, *R. auricomus*, *R. abortivus*, *R. sceleratus*, *R. multifidus*, *R. acris*, *R. polyanthemos*, *R. lanuginosus*, *R. repens* and *R. bulbosus*.

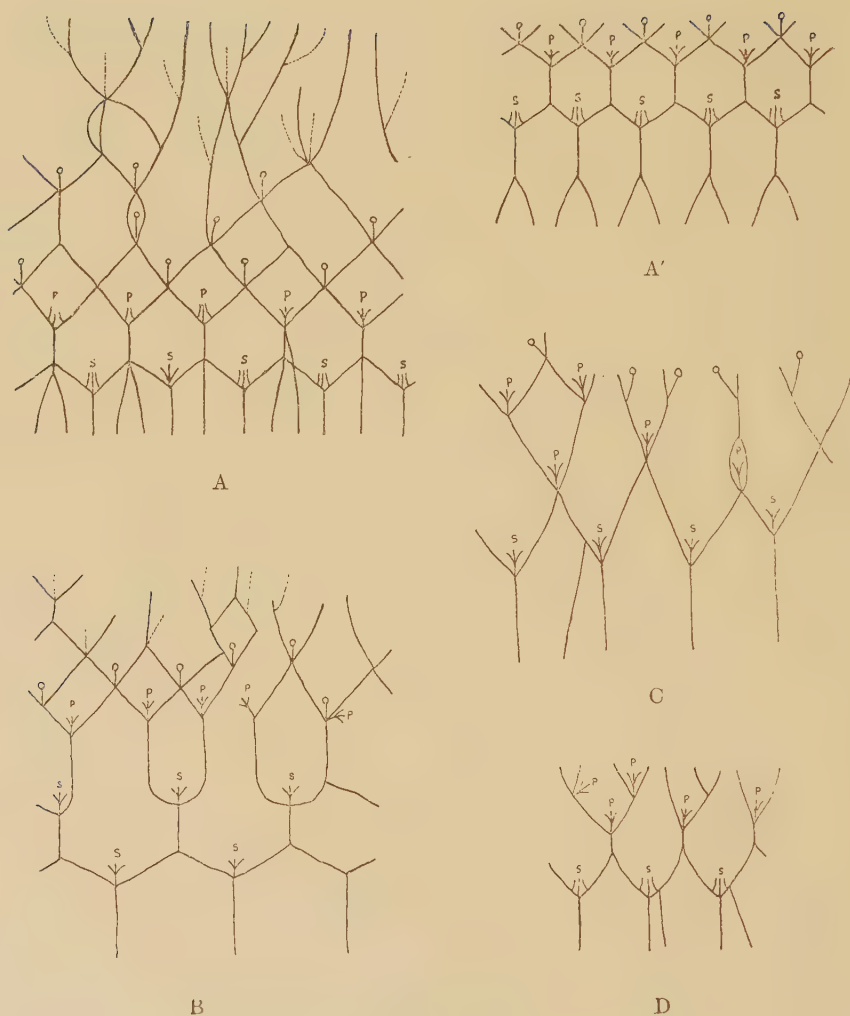
layer described as of common type by MARIE, may probably be the outermost layer of the interfascicular fibrous cylinder as already suggested by JEFFREY (1899) from the seedling anatomy of the group.

The vascular system of the rhizome consists of separate vascular strands or of the vascular cylinder as already mentioned; in the former case the endodermis encloses completely each vascular strand or a group of the strands respectively, while in the latter both the external and internal endodermis may be recognized, although they may or may not communicate with each other through the leaf gaps. The endodermis of the slender species is characterized by the lignified Casparian strips alone without further differentiation; but in the vigorous species the cell walls of the endodermis, except a few cells which remain parenchymatous and seem to be analogous to the passage cells of the root, tend to become thickened and lignified on all their sides and the difference between the endodermal and the mechanical pericyclic layers may disappear. In the rhizomes of *R. Tachiroi*, *R. Vernyi*, *R. chinensis*, *R. japonicus*, *R. acris*, *R. yaegatazensis*, *R. Kawakamii*, *R. yakushimensis*, etc., the internal endodermis is scarcely recognizable or it develops very slightly, if it does occur, while the external one is very evident.

As this endodermal tendency was first described and discussed phylogenetically by JEFFREY (1899) in the plumular anatomy of *Ranunculus*, it is, therefore, unnecessary to be discussed further here.

V. COURSE OF VASCULAR SYSTEM IN THE FLORAL ORGANS

In the peduncle the vascular strands run almost parallel to one another and their number varies even in one and the same species; but generally speaking, it is about ten in *R. Vernyi*, *R. chinensis*, etc., in which however they are reduced to five at the top of the peduncle; and it is about five in *R. acris*, *R. japonicus*, *R. Zuccarini*, *R. aquatilis*, etc., and three in *R. Kawakamii* and *R. flagellifolius*. In the floral receptacle these strands anatomose somewhat irregularly, producing the traces of the sepal, petal, stamen and carpel. From the careful study upon these vascular distributions by the cross section, the writer found it difficult to present any general interpretation of the result, because the vascular distributions are extraordinarily divergent and are hard to understand the ground plan even in one and the same species.



Text-fig. 8. Diagrams showing the floral vascular distribution.

A, A': *R. Vernyi*. A', typical feature. A, the difference of the vascular supply between the sepal and petal traces is not clear in this example.

B: *R. flagellifolius*. Sepal traces occur from two different levels and are similar to the petal traces in their vascular behaviour.

C: *R. Zuccarini*, an abnormal flower with 4 sepals and 6 petals. Stamen traces do not occur at the point of the vascular bifurcation.

D: *R. acris*, an abnormal flower with 3 sepals and 5 petals.

In all the diagrams, only lower parts of the floral receptacle are shown.

s, sepal trace. p, petal trace. ♂, stamen trace. dotted line, carpel trace.

SMITH¹²⁾ (1926), studying normal flowers of *R. hispidus* and *R. septentrionalis* and lately (1928) the double flowers of those species, came to the conclusion on the floral vascular course that the sepal of *Ranunculus* flower is supplied with three strands, each of which occurs from the different point of the receptacular bundles respectively, quite contrary to the petal traces which consist of a trilobed strand, supplied from one point of the floral receptacle; and also that the petals which are similar to the sepals in their vascular occurrence, may have probably been derived originally from the stamens among this genus (see GLÜCK, 1919; pp. 498-499).

In the present study, nevertheless, the writer found two important types in the sepal traces of this genus. The sepal traces of *R. acris* (Text-fig. 8; D, s), *R. japonicus*, *R. Vernyi* (Text-fig. 8; A, A', s), *R. chinensis*, *R. sceleratus* (Text-fig. 9; upper part of the photograph), *R. aquatilis*, etc., come out from three different points of the receptacular bundles and are clearly different from the traces of petals (Text-fig. 8, p; Text-fig. 9, lower part of the photograph) as SMITH observed, although some traces of the sepals are abnormally supplied with a single strand and become trilobed afterwards as those of the petals, but even in such cases the difference between the sepal and petal traces can be easily recognized, because such sepal traces, occurring from a point of the floral vascular skeleton, divide into three already at the innermost part of the receptacle, while the petal traces divide into three at a rather peripheral part of it.

On the other hand, in the case of *R. Kawakamii*, *R. flagellifolius* (Text-fig. 8; B, s) and *R. yatsugatakensis*, the sepal traces are unilacunar as in the case of the petal traces, occurring from a point of the floral vascular skeleton and they divide further afterwards into three in the same way as the petal traces do, so that any difference between the sepal and petal, as far as the vascular behaviour is concerned, can not be observed.¹³⁾ The relation between the different textures of the sepal traces mentioned above, is left untouched in this paper. The petal, the stamen and the carpel are all unilacunar in their vascular behaviour, occurring from a point of the floral vascular skeleton (Text-fig. 8).

12) Besides SMITH, HENSLOW (1889; p. 155, pp. 165-166) and BUSSE (1914; pp. 13-14) studied the vascular distribution of the floral receptacle and of the floral leaves of *Ranunculus*. The latter author divided the perianth of Ranunculaceae into three types with reference to the vascular behaviour.

13) But, of course, both floral leaves can be clearly distinguished by the external features and the mode of their development.

The mode of the anastomosis of the floral vascular bundles varies extraordinarily, but in the most typical case (Text-fig. 8, A'), the strands in the peduncle bifurcate into two at the basal part of the receptacle, producing the sepal traces (s) at the point, and each bifurcated strand meets



Text-fig. 9. Cross section of the floral receptacle of *R. sceleratus*. A sepal trace (upper part of the photograph) consists of different three strands contrary to a petal trace (opposite side of the sepal trace) which divides into three at the peripheral part of the receptacle. ($\times 40$)

with each other at the point just between the two adjacent sepals at the higher level, and at this point the strand divides also into two, producing petal traces (p) between the two. Such a feature may be regarded as typical in *R. Vernyi*, *R. Zuccarini*, *R. chinensis*, *R. aquatilis*, etc.; but sometimes in other species, for example in *R. Kawakamii*, the petal traces do not occur at the bifurcated vascular point.

Sepals or petals never come out from the same level exactly but rather irregularly; i. e. in *R. flagellifolius* (Text-fig. 8; B, s) five sepals in a flower occur, as arule, from two different levels of the receptacle:

two sepals from the lower and remaining three from the higher level.

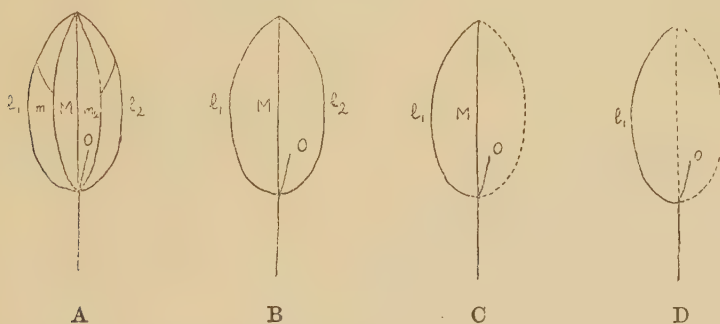
Stamen traces¹⁴⁾ appear usually without dividing into three, though not always, at the point of the vascular bifurcation as in the case of the petals.

As for the carpelar vascular distributions which were studied more or less accurately by ADLERZ (1884)¹⁵⁾ and LONAY (1901), several modifications are observed in this genus. In *R. Vernyi* and others (Text-fig. 10, A), one strand enters into the carpel from the floral receptacle and then it divides into five (l_1 , m_2 , M, m_2 , l_2) at a point, from which also an

14) In most examples studied, the spiral arrangement of both the stamen and the carpel could not accurately be traced by their vascular distribution in the reconstructed diagrams of the cross sections.

15) ANDLERZ (pp. 39-40) divided anatomically the pericarp of Ranunculaceae into three groups 'Paeoniatypen,' 'Ranunculustypen' and 'Thalictrumtypen.'

ovular bundle¹⁶⁾ develops; these five bundles consist of one midrib M and four lateral nerves, all of them connecting at the end of the carpel to one another. In most species (Text-fig. 10, B) a pair of the lateral nerves m_1 and m_2 does not develop; but further l_1 and l_2 fuse into a single strand in *R. nipponicus* (Text-fig. 10, C). Such an example is rather rare in *Ranunculus* except *R. divaricatus*¹⁷⁾ described by LONAY. The writer found the most reduced example of the carpelar vascular distribution in *R. aquatilis* (Text-fig. 10, D). In this species, at least in the materials studied, even the midrib M disappeared and only a single lateral nerve l_1 , from which the ovular bundle seems to occur, is recognized.



Text-fig. 10. Diagrams of the carpelar vascular course. A, *R. Vernyi*. B, most usual type. C, *R. nipponicus*. D, *R. aquatilis*.

Broken line denotes the fused strand. o, ovular bundle.

In short, the carpel of *Ranunculus* is, in the typical case, provided by three strands which come out as a single strand from the receptacle as petal traces do, but in some cases the gradual vascular reduction or amplification is observed in the pericarp.

VI. HISTOLOGY OF THE FLORAL ORGANS

The histological structure of the peduncle is similar, in general, to that of the stem, but is rather simple. The endodermis of the peduncle is not distinct, as a rule, in *Ranunculus* except the submerse species which have the individual one, though MARIÉ (1884, p. 83) described the common endodermis even in the species which have the individual

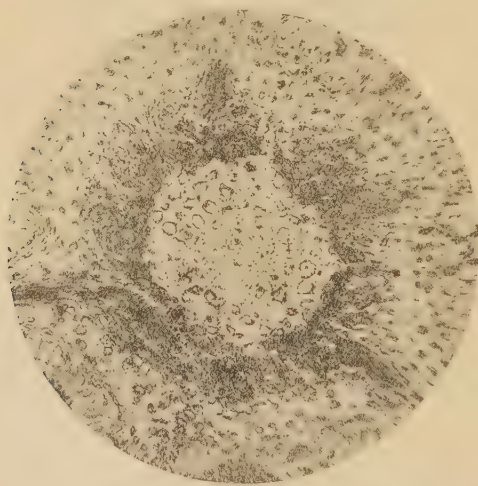
16) According to KÜHN (1926) there is no intraseminal bundle in the ovule of Ranunculaceae except a genus *Anemone*.

17) This species is also submerse one, belonging to the section *Batrachium*.

one in the stem, but his description seems to the writer doubtful as already mentioned.

Among some species such as *R. Vernyi*, etc., the peduncle increases both its length and diameter, and afterwards even the amounts of the chlorophyll bodies for the purpose of the fructification. Such a secondary growth is more evident at the upper part of the peduncle and also at the lower part of the floral receptacle from which the sepal and petal traces may appear. In a cross section of the basal part of the floral receptacle, the vascular bundles may fuse almost with one another to form a vascular cylinder in *R. acris*, *R. chinensis* (Plate II, Fig. 15) and *Batrachium* (Text-fig. 11, *R. aquatilis*), thus presenting the siphonostelic appearance, particularly in the older stage; while they may not fuse, as observed in the stem, in the case of *R. sceleratus*, *R. Kawakamii*, *R. flagellifolius*, *R. altaicus*, etc.

Now let us compare the bundle structure of the upper part of the peduncle with that of the floral receptacle. In the bundles of both organs



Text-fig. 11. Cross section of the basal part of the floral receptacle of *R. aquatilis*. Internal pericyclic or endodermal cells are thick-walled. ($\times 50$)

the secondary elements are clearly produced in both directions, being arranged in radial rows. The xylem presents no more V-shape and moreover the bundle is not enclosed by the bundle sheath. At the upper part of the peduncle the secondary vessels are rather small and uniform in size and are scattered diffusely among rather great amounts of the xylem parenchyma, and the phloem develops more considerably as shown in *R. yatsugatazensis* (Plate II, Fig. 13).

On the other hand at the floral receptacle the secondary xylem elements, produced later, become larger and larger in size in the radial direction without comprising any parenchymatous cell among them (Plate II, Fig. 14, *R. Vernyi*; Fig. 15, *R. chinensis*), but the several layers of the secondary vessels produced at the younger stage of the receptacle, lose their cell contents being parenchymatous for a time, and then their walls are suddenly lignified almost at the same time when the seeds come to maturity.

Whether the occurrence of the vascular cylinder and of the great amounts of the secondary elements in these conservative organs of some species, is due to the phyletic character or to the physiological requirement, can not be carelessly discussed at present; but it is briefly suggested that the occurrence of this feature seems not to be explained by the physiological or ecological requirement alone, because this feature appears in some species, including even the submerse species in which the lignified elements are usually poor in development, while it does not appear in other species of the land form.

In general, the fibrous sheath of the bundle, prevalent in other organs, can not be observed in the receptacle, but the writer found some mechanical elements at the peripheral part of the pith of the floral receptacle in *R. chinensis* (Plate II, Fig. 15) and in *R. aquatilis* (Text-fig. 11). Although the origin of those elements in the former species was not traced, the fibrous ring found in the latter species was ascertained to consist of the cells of the internal endodermis and of the pericycle whose cell walls are lignified and uniformly thickened at all points. Such a feature was not observed from any plant in this genus. In *R. aquatilis* the vascular cylinder is separated again into some individual strands at the upper part of the receptacle from which the carpel traces may occur; the common endodermis, therefore, becomes individual, but in all other species the endodermal layer is not distinct in the floral receptacle except in *Batrachium*.

VII. STRUCTURE OF THE ROOT

All the roots of the adult plant, adventitious in their origin, are filiform, 10–15 cm. or more in length, occurring from all the sides of the rhizome except in *Batrachium* which has no specialized rhizome.

Ontogenetically speaking, several adventitious roots develop already at the cotyledonar node of the seedling which has a few leaves, and the absorbing function of the seedling seems to be due to them, therefore the principal root does not develop further and soon decays away in all the species studied, contrary to the case of *R. arvensis* described by NIHOUL (1890). In *R. Zuccarini*, the adventitious roots often metamorphose themselves to the tubers from their first developmental stage.

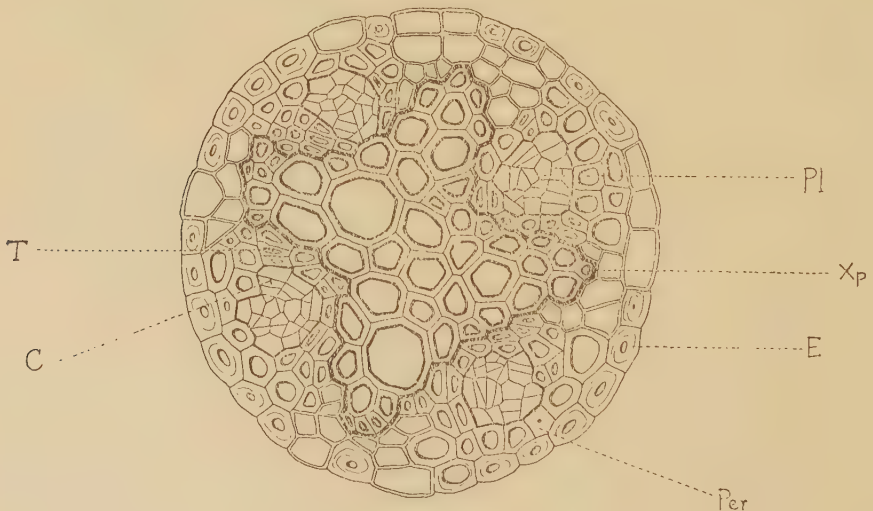
All the walls of the epidermal cells are uniformly suberized in the old roots, losing their protoplasmic contents, being brown in color, but they do not peel off from the outermost cell layer of the cortex. Cortical cells may contain great amounts of the starch grains and sometimes

mycorrhizas in younger stage, but the cell contents are lost in the later stage and soon the cortex may be destroyed, being occupied by large lysigenous spaces.

The central cylinder is nearly $1/6$ of that of the root proper in diameter and that of the adventitious roots of the first order is usually tetrach, in the vigorous species such as *R. Vernyi*, *R. chinensis*, *R. japonicus*, *R. acris*, etc., and usually triarch in *R. sceleratus*, *R. yatsugatazensis*, *R. altaicus*, etc., and diarch in the slender species such as *R. flagellifolius*, *R. Zuccarini*, etc. The rootlets of the second order and the principal root of the seedling are always diarch in all the cases studied. The branching of the lateral rootlets occurs always from the pericycle near the xylem part as usual in all the dicotyledonous roots, and metaxylem meets at the centre of the cylinder.


Concerning the adventitious roots of *Ranunculus*, the radial thickening of the central cylinder was described by MAXWELL (1893, p. 44) only in *R. sceleratus*, while it was not observed in the adventitious roots of the species used in this study.

When the roots of *R. Vernyi*, *R. chinensis*, *R. acris*, and *R. japonicus* become old, some lignified elements increase in rows on both radial and



Text-fig. 12. Central cylinder of the older adventitious root of *R. acris*. Some cells of both endodermis and pericycle are thick-walled. Between the phloem and the xylem, small amounts of the secondary elements (T) are produced by cambium, but the secondary growth of the central cylinder is not recognized.

Per, pericycle. E, endodermis. P, phloem. Xp, protoxylem. ($\times 160$)

inner tangential sides of the phloem (Text-fig. 12, T), so that the xylem presents a shape such as . This feature is described by DE BARY (1877) in *R. repens*, by NIHOUL (1891) in *R. arvensis*, by SARTON (1905) in *R. Duriaei*, etc., and is due to very reduced cambium which is not so active as to increase the diameter of the central cylinder. Corresponding to the modification of the xylem part as mentioned above, the uniform thickening and lignification of the cell walls of endodermis and of pericycle occur a little later except a few endodermal and pericyclic cells which are opposite to the xylem. The thickening of the endodermal cell walls is one of the prevalent features among monocotyledonous roots as already shown by DE BARY (1877) and is not common in dicotyledonous ones, although it was described by him in *Primula auricula* and *R. repens*, by MARIÉ (1884) in many species of *Ranunculus*, by JANCZEWSKI (1897) in *Hepatica* and *Anemone*, by SARTON (1905) in *R. Duriaei* and *R. bulbosus*.

It is worthy of note that in the adventitious roots of *R. chinensis* the pericyclic cells which are opposite to the xylem are often radially elongated and consist of large parenchymatous cells contrary to those of other parts. Such a modification of the pericyclic cells has not been described in any plants as far as the writer knows, but the development and significance were not studied.

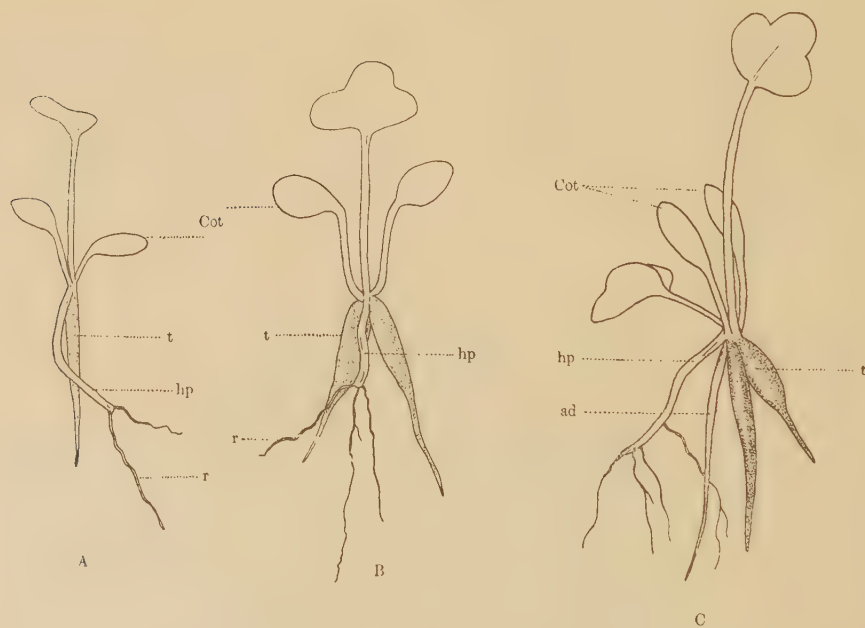
VIII. TUBER OF *RANUNCULUS* ZUCCARINI MIQ.

In some species of *Ranunculus* such as *R. bulbosus*, *R. chaerophyllos*, *R. Ficaria*, *R. asiaticus*, *R. monpeliacus*, *R. pedatus*, *R. hybridus*, *R. illyricus*, *R. millefoliatus*, etc., the subterranean tubers are produced and were studied biologically or morphologically by various authors; among these species *R. Ficaria* was most fully studied particularly by IRMISCH (1854, 1865), VAN TIEGHEM (1866), ASELMANN (1910) and HALKET (1927).

According to the above mentioned and other authors, the tubers of *Ranunculus* are represented by the modified adventitious roots, developing from the subterranean parts of the stem and they store great amounts of the starch grains. After the aerial parts of the plant give off, the tubers are dominant, and produce the aerial organs in the subsequent growing period, but in *R. Ficaria* the tubers may develop at the node of the aerial stem and separate from the mother plant; a bud on that tuber develops in the autumn of the same year, producing foliar leaves. According to the description of STERCKX (1899,

pp. 42-48), the germination of the seed of this species is extraordinarily slow. A cotyledon and an adventitious root appear in the third year after sowing, the adventitious root becoming a small subterranean tuber and any aerial leaf or adventitious root does not, as a rule, develop in that year. But among 35 seedlings, he found only four plantlets which were provided with the first aerial leaf and the second adventitious root in that year in which the cotyledon has appeared. This second adventitious root was not tuberous.

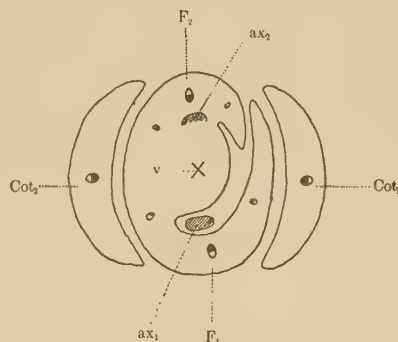
Now permit the writer here to describe the tuber of *R. Zuccarini*, the only Japanese species with tubers. Two kinds of the adventitious roots are observed also in the species as usual, the one normal filiform absorbing root and the other its modification or the tuber. The tubers



Text-fig. 13. Seedlings of *R. Zuccarini* in the first year of their germination, showing the development of the tubers. Cot, cotyledons. t, young tubers. hp, hypocotyls. r, primary roots. ad, adventitious roots. ($\times \frac{2}{3}$)

are usually of the spindle form, 4 mm. in the greatest diameter, 10 mm. in length, and are found all around the base of the subterranean stem, being three to eight in number (Text-fig. 15, T). The germination of the seed and the development of the seedling show no morphological or biological peculiarity contrary to the case of *R. Ficaria*, and the

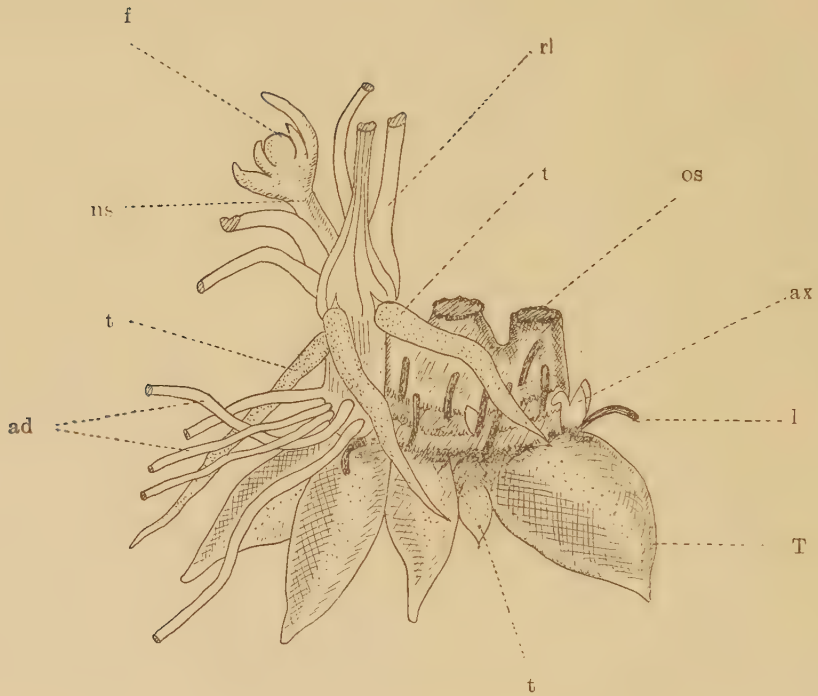
seedling with a rather long hypocotyl produces several adventitious roots and aerial leaves in the first year of its germination (Text-fig. 13). The first and second adventitious roots which occur from the cotyledonar node of the seedling, become rather slender tubers (Text-fig. 13. t), increasing their diameter and storing the starch grains in the cortical tissue. These two tubers are theoretically the adventitious roots which arise from the basal parts of the first and the second foliar leaves respectively, and these two leaves are almost opposite to each other, each of which subtending an axillary bud of its own (Text-fig. 14, ax). Besides the tubers, a few absorbing roots may also be produced (Text-fig. 13, ad). This is the seedling of the first year of its germination, and the aerial parts of the plants die away entirely in early June, but in March of the subsequent year one of the axillary buds (Text-fig. 14; ax_1 , ax_2) becomes dominant,



Text-fig. 14. Cross section of the seedling epicotyl of *R. Zuccarini* with two foliar leaves (F_1 , F_2). ax, axillary buds; one of these buds, from whose base the first two tubers appear respectively, becomes dominant in the following spring. v, dormant vegetative point. ($\times 15$)

producing some foliar leaves with the aid of the reserve materials in the tubers, so that the old tubers shrink and wither losing their contents, but soon several new tubers appear in the neighbourhood of the old tubers or at the base of new foliar leaves, being accompanied with the axillary buds respectively, some of which become dominant in the third year and so on. The erect stem with flowers may not yet be produced usually in the second developing period by reason of rather small amounts of the reserve materials, but after a few years the tubers increase in number, producing several stems which terminate in flowers (Text-fig. 15, os).

The tubers of this species do not separate from the subterranean parts of the mother plant but are in contact all the time firmly to the mother plant, forming a cluster of tubers, and also they are not produced at the node of the aerial stem. In these respects the tuber of this species and that of *R. Ficaria* are most clearly different, but in *R. Zuccarini* if the perennial basal part of the stem is planted rather deeply into the ground, several internodes may develop in the



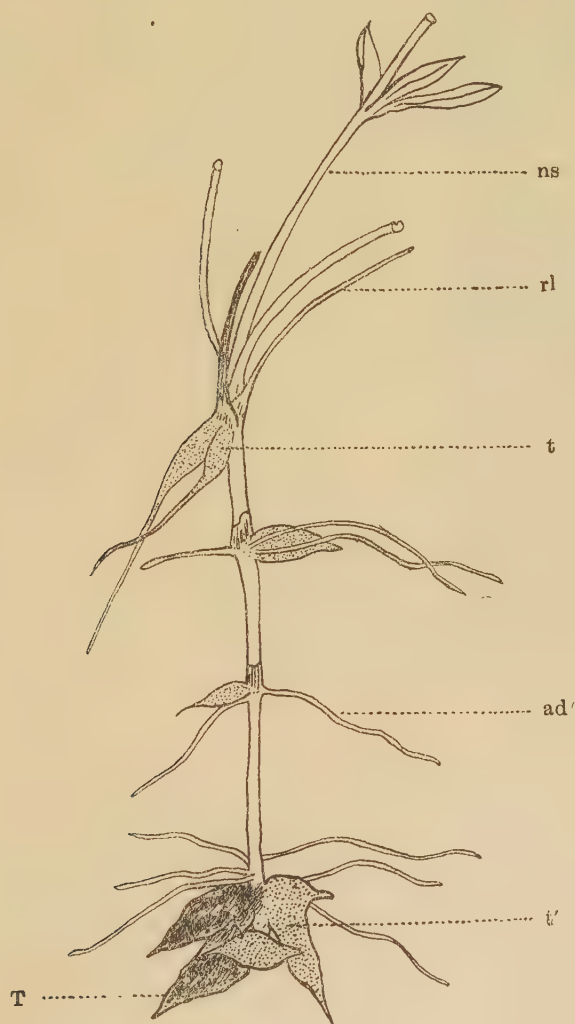
Text-fig. 15. An old plant of *R. Zuccarini* in early spring, new erect stem (ns) with floral bud occurring from one of the axillary parts of the Dizome. ad, adventitious roots. l, remains of the petiolar strands of the foregoing year. t, new tubers. T, tubers now withering. os, stems of the foregoing year. rl, radical leaves of this year. ($\times 4$)

ground until the elongated stem becomes aerial. In such a case new tubers develop at each subterranean node of that stem, being accompanied with usual absorbing roots as shown in Text-fig. 16, and the radical leaves (Text-fig. 16, rl) are not produced from the nodes situated rather deeply in the ground but from the nodal region which is the uppermost in the ground.

As already described, most tubers are of the spindle shape, one end attaching to the mother stem and the other presenting the growing point, but some have two free points, presenting a curious shape by the branching of the growing tubers (Text-fig. 16, t').

The thickening of the tuber is due only to the expansion of the

cortical cells by storing starch grains but not to any secondary cell division as described in other tubers of this genus. The cell walls of the



Text-fig. 16. Abnormally induced tubers.
Abbreviations as in Text-fig. 15. Explanation in
text. Slightly enlarged.

epidermis and of an outermost cortical layer are usually cutinized, losing their cell contents, becoming brown in color as in the case of other species, but in this species there are neither epidermal hairs nor



Text-fig. 17. *R. flagellifolius* without stolons.
Slightly reduced.

'cellules de passage' named by JANSE among the hypodermal layers. Except these two cutinized layers and the endodermis, the cortical cells store great amounts of the starch grains from the first developmental period of the tuber. As for the mode of the starch transfusion in the tuber, HALKET (1927) made an interesting study on the tubers of *R. Ficaria*; according to him the stored starch grains disappear at first in the central part of the cortical tissue and the disappearance goes on inwards in the direction of the endodermal layer and outwards in that of the hypodermal layer, but in the present species this point was not ascertained.

Endotrophic mycorrhizas are often found in the innermost cell layer of the cortex of the absorbing roots but not in the case of the tuber.

The central cylinder is usually diarch both in the absorbing root and in the tuber; the endodermal cells are thin-walled and are left unchanged.

IX. LEAF OF *RANUNCULUS FLAGELLIFOLIUS* NAKAI

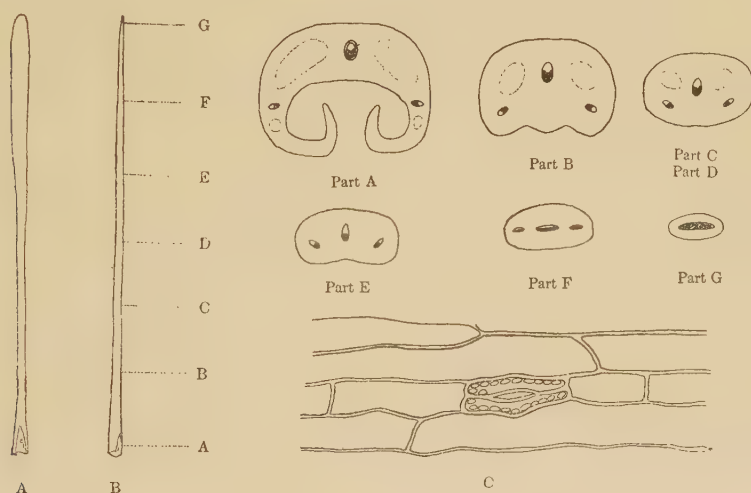
The leaf of *Ranunculus* consists usually of the lamina, petiole and leaf sheath, and the compound lamina of land forms is three-lobed or somewhat modified. The sheath envelops the stem all around or partially. The structure and the development of the leaf of Ranunculaceae have already been described from various points of view in full detail, particularly by BITTER (1897), LONAY (1901) and SCHRÖDINGER (1914), so that there seems no room to be left for further studies, but permit the writer for a while to describe the structure of the leaf of *R. flagellifolius* which has the creeping stems and occurs at the wet ground in Japan.

Apparently monocotyledonous leaf¹⁸⁾ of this endemic species (Text-

18) Quite similar features of the leaf are observed also in an European species *R. Flammula* L. var. *reptans* SM. to which present species is most closely related and was once regarded as identical.

fig. 17, Text-fig. 18, B) is filiform, about 2–12 cm. in length and 1–2 mm. in width, traversed by three parallel vascular strands in the mesophyll. Leaf sheath is less than 1 cm. in length enclosing very short rhizome. No differentiation between the lamina and the petiole is usually observed.

The epidermal cells, whose external surface is provided with very minute cutinized furrows in a longitudinal direction, are long, being parallel to the nerves of the leaf. Stoma is somewhat elevated from the epidermal level, their guard cells being rather elongated in the longitudinal direction (Text-fig. 18, C).



Text-fig. 18. Leaf of *R. flagellifolius*. A, abnormal leaf with lamina-like part. B, normal leaf. C, stoma and epidermal cells of a normal leaf. Part A . . . part G, cross section of the normal leaf. Explanation in text. A, B; slightly reduced. C, $\times 300$

On cutting a leaf at seven different levels in parts A, B, C, G, from the base upwards (Text-fig. 18, Part A Part G), the following different structures are recognized in the cross section:

PART A. Epidermal cell walls are cutinized on the external side and are rather thickened. No cutinized furrow is found except the surface of the epidermis near the phloem side of the midrib. Fundamental tissue, consisting of round parenchymatous cells, contains many large lysigenous intercellular spaces except the subepidermal layers and the peripheral parts of the bundles, and in the tissue no differentiation between the spongy and palisade tissues is found and the chlorophyll bodies are scarcely observed. The structure of the bundle which has a bundle sheath is similar to that of the stolon.

PART B. Lysigenous spaces become smaller, while the schizogeous spaces increase and the fundamental tissue contains more numerous chlorophyll bodies.

PART C. PART D. The lysigenous spaces occupy a very small area. The differentiation of the sponge-like tissue occurs at the cortical part which is ventral to the midrib.

PART E. The lysigenous spaces give off here. All of the fundamental tissues consist of the sponge-like assimilatory tissue and the bundle sheath disappears.

PART F. The fundamental tissue consists of round parenchymatous cells and it does not contain any intercellular space. Epidermal cells become rather large and their walls thicken themselves to a certain extent. The vascular strands are flattened from both sides, and are diminished in volume.

PART G. The phloem part is reduced entirely in each strand. The three different strands fuse together laterally to form a single strand, then the terminal part connects with the waterpores.

The leaf with such characteristic features and appearance is an exceptional one in Ranunculaceae, and at the first glimpse one may suppose it to belong to a Monocotyledon, but it is interesting to note here that under some conditions somewhat modified leaves¹⁹⁾ may appear, whose terminal parts present very reduced lamina-like appearance as shown in Text-fig. 18, A instead of the ordinary filiform leaves. This abnormally modified part is 3 mm. in width and 20 mm. in length in the most developed example. The upper epidermal layer of the lamina-like part consists of the elongated parenchymatous cells and of stomata, which are parallel to the nerves in their arrangement, and the cells of the lower epidermal layer show the wavy outline in surface view as in the case of other land forms. The cross section of the part shows that the mesophyll consists of 7-8 cell layers; among them the cells of the upper three layers are somewhat regular in their shape and contain somewhat more abundant chlorophyll bodies than those of the lower layers. Besides these, no differentiation among them can be observable. At the lamina-like part mentioned above, the original three nerves may be divided into five to seven usually, and run almost parallel to one another through that part.

These features suggest that the lamina-like part, though it occurs rarely, may be a real lamina which is usually in reduction, and further

19) The variation of the shape of leaves is often found in one and the same species of *Ranunculus*.

that the filiform part of the normal leaf may not be homologous to the petiole without lamina, but may be a modification of an usual leaf with both the petiole and the lamina.

It is quite probable that this characteristic leaf of *Ranunculus flagellifolius* may be derived phylogenetically from the leaf with laminar and mesophyllar differentiations. This may be the reason why the abnormal leaves described above may often appear.

X. RELATIONSHIP AMONG THE SPECIES STUDIED

From the foregoing anatomical study on 16 species of Japanese *Ranunculus* they may be divided conveniently into five groups as shown in Table III:

TABLE III.

| | |
|---|--|
| (IV) <i>R. aquatilis</i> <i>R. nipponicus</i> | (V) <i>R. chinensis</i> <i>R. Tachiroi</i> <i>R. Vernyi</i> <i>R. japonicus</i> <i>R. acris</i> <i>R. yakushimensis</i> <i>R. yaegataakensis</i> |
| (III) <i>R. Kawakamii</i> <i>R. flagellifolius</i> | |
| | (II) <i>R. pygmaeus</i> <i>R. yatsugataakensis</i> <i>R. altaicus</i> <i>R. Zuccarini</i> |
| (I) <i>R. sceleratus</i> | |

GROUP I.

Biennial species with the vigorous erect stem, growing in rather wet ground. Leaf sheath is narrow in width, enclosing a small part of the stem surface, and vaginal stipules are often recognized (GLÜCK, pp.

127, 201). Petiole dorsiventral, not unifascial. Leaf trace strands are few in number, usually three, each of them being of the Type A. The vascular bundles of the full-grown stem are of the typical Anemone Type and some amounts of the secondary xylem may be produced. The xylem does not present mostly the typical V-shape. All these characters are probably more primitive ones among this genus.

GROUP II.

Rather slender species, mostly found in the alpine region of Japan, except *R. Zuccarini*. Root and leaf, simple in structure and similar to GROUP I. Petiole dorsiventral; a petiole contains three strands, the middle one of which is of the Type A. A protecting fibrous are of the stem bundle may or may not occur only on the phloem side, but it may or may not often show a tendency to elongate in the direction of the xylem. In this regard this group seems to be the transitional form between GROUP I and GROUP III.

Generally speaking, among the plants of this group, reducing tendencies caused by the surrounding factors are to be observed in the vegetative organization except in the fibrous sheath. *R. Zuccarini* might or might not be included in GROUP I, for this species is related to *R. sceleratus* in some respects, while the former differs from the latter in the reduced bundle behaviour and the small amounts of the secondary xylem elements.

GROUP III.

Slender species with the creeping stolons. The great influence of the adaptative tendency, namely that of the water habit, must not be over-looked. Vascular strands in the stem and peduncle are greatly reduced in number. The feature of the leaf trace is similar to that of the former group. The difference between the sepal trace and petal trace is not found. The bundle sheath may develop on both the xylem and the phloem sides, but they do not elongate far enough to enclose the strand all around, therefore it may show the transitional form between the Anemone and the Ranunculus Types.

GROUP IV.

Submerse species with white petals. Bundles are often surrounded by extremely reduced mechanical layers in older node, suggesting those of the reduced Ranunculus Type. The feature of the leaf trace is similar to the former group. Xylem is occupied by a schizogeous cavity. Storage organs do not develop.

GROUP V.

Perennial or biennial plants with erect stems, bundles being of the typical *Ranunculus* Type enclosed by the thick monocotyledonous bundle sheaths. Secondary xylem elements are greatly reduced. The vascular strands in the stem increase extraordinarily in number in the vigorous species. The number of the leaf trace strands of the Type A, three to nine in general. Petiole is, as a rule, unifascial but in a few cases dorsiventral. This is, in all probability, the group most specialized as the land form.

The above mentioned grouping founded on the present anatomical study seems to coincide, to some extent, with the taxonomical subdivision of the genus considered.

In the foregoing pages, the writer has made a study upon the structure of *Ranunculus* which is regarded as one representative genus among the Ranunculaceae, but just a few words should be said, in general, regarding these species. The structural and morphological divergences among these species seem to be induced mostly by the adaptative or environmental factors, particularly by the water of the substratum on which one species habitually grows, and further the majority of the various characteristic features in one species seems also to be correlated to the degree of the aquatic habit of the species, but some of them may more properly be considered as the phyletic ones.

XI. SUMMARY

1. Sixteen species of *Ranunculus* found in Japan were studied both morphologically and anatomically.

2. Stem habit and its modifications were described: *R. Kawakami* has two kinds of the stem, the one being erect bearing flowers, and the other a long stolon without terminating in flowers. From every node of the latter develops an individual plantlet. *R. flagellifolius* is lacking the erect stem and the flowers appear from the nodes of the slender creeping stem.

3. Vascular course of the stem was traced in many species; that of the vigorous species is rather complicated in its behaviour on account of the great numbers of the leaf trace strands and the divergence of the vascular courses does not suggest any phyletic relationship in this group of plants studied. Two types of the leaf trace strands were found; the one, Type A, denotes the strands which run from the petiole downwards without fusing, as a rule, with any stem strand at least in

the next internode; and the other, Type B, those which join with the stem strands immediately after their entering into the stem. The strands of these two categories were examined in each species and their behaviour and significance were discussed.

4. The ontogeny of these strands was studied and two nodal conditions were found: in the seedlings of most of the species, each of three leaf trace strands, belonging to a leaf, forms the gap of its own, while in those of *R. Zuccarini* three strands leave only a common gap upon the central cylinder.

5. It would seem that in this genus the trilacunar and unilacunar conditions of the node are closely related to each other. The one condition may change easily to the other even in the same plant by the dislocation of the point of exit of the leaf trace strands or by the partial fusion of the leaf trace strands with the stem strands or also by the new appearance of the leaf gaps.

6. The rhizome is very short and usually of a cannon-ball shape, storing starch grains, but in some species it is pretty long and rather small in diameter. Stem bundles fuse closely with one another in the rhizome, forming the vascular cylinder provided with the external and internal endodermis. Both endodermal layers communicate through the leaf gaps, but the tendency towards reduction of the internal one was often observed.

7. Vascular course in the floral organs was also traced, but it was sometimes extraordinarily irregular even in one and the same species. The sepal and petal are clearly distinguished, in general, by their vascular distribution, but in several species such as *R. Kawakamii* and *R. flagellifolius* they are quite similar to each other.

8. Stem bundles are, in some species, entirely surrounded by thick mechanical sheaths, so that the cambial activity is greatly disturbed. Such a sheath is not common in dicotyledonous bundles, but is prevalent among monocotyledonous ones and was named here as 'Ranunculus Type.' On the contrary, the bundles of *R. sceleratus* and others are not surrounded by such sheaths, and do not even show such a tendency, hence the secondary thickening may be possible. These bundles, rather rare in *Ranunculus*, was called as 'Anemone Type.' This type seems to be probably more primitive than the former one in this genus.

9. The characteristic V-shape of xylem, found usually in the stem bundles of this family and very prevalent in Monocotyledons, seems to

appear by the reduction of the cambium and the formation of rather big cells at both lateral parts of the primary xylem.

10. The stem bundle has the individual endodermis even in the species which have already been described as having a common one, moreover the species with the common endodermis were never found during the course of this study, so that the writer is inclined to believe that the bundles of *Ranunculus* may always be astelic in the aerial stem.

11. In the floral receptacle of *Batrachium*, the individual or common endodermal layer is clearly recognizable by the Casparian strips, although it is not distinct in the organ of other land species.

12. At the upper part of the peduncle or at the lower part of the floral receptacle of some species, the vascular strands fuse often with one another laterally and the xylem presents no more the V-shape. In these organs and the rhizome, the secondary thickening of the central cylinder is observed, though such a feature, as a rule, never occurs in the ordinary stem.

13. Amphivasal concentric medullary bundles which were hitherto unknown from this genus were found abnormally in the aerial stems of *R. chinensis* and *R. Vernyi*.

14. The leaf of *R. flagellifolius* is linear in shape and suggests that of the monocotyledonous plant with parallel leaf nerves. Mesophyllar differentiations do not develop. The leaves with somewhat broader lamina-like part appear quite abnormally. This seems to show a type of the leaf from which the characteristic filiform leaf of this species might be derived phylogenetically.

15. The principal root dies away early in the seedling and numerous filiform adventitious roots, whose central cylinder or fundamental tissue does not increase their diameter, occur from the short rhizome. The cell walls of the endodermis and of the pericycle become thickened and lignified in the adventitious roots of some vigorous species. Endotrophic mycorrhizas are found in some species in an innermost cell layer of the cortical tissue.

16. The morphology and the development of the tuber of *R. Zuccarini* were described.

17. Judging from the results of the comparative study of 16 species of Japanese *Ranunculus*, it seems to the writer probable that the environmental condition, particularly the water of the substratum, exerts the greatest influence upon the appearance of the structural divergences, but if phylogenetically considered from various points of

view mentioned in this paper, *R. sceleratus* may be regarded probably as one of the most primitive representatives of this genus.

In closing, the writer wishes to express his sincere thanks to Professor Y. OGURA of this Institute, now in Europe, for his criticism and reading of the manuscript and to Emeritus Professor K. FUJII and Professor K. SHIBATA for their kindness in publishing this paper.

He also desires to record his obligations to Professor T. NAKAI and other systematists who have kindly furnished him the taxonomic data contained in this study and to Drs. Y. TAKENAKA, E. YAKUSHIJI and G. MASAMUNE who have so kindly supplied him with some of valuable materials.

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(* denotes the works which were not consulted in the original.)

XIII. EXPLANATION OF THE PLATES

PLATE I

Diagrams showing the course of the vascular system in the stem or stolon of Japanese *Ranunculus*, made from the macerated material or the reconstruction of the cross sections. Surface view.

The leaf trace strands and the points of their exit are denoted by \bullet , \circ and \odot . Among them the first one denotes the strands of the Type B; the others, those of the Type A; the last one, the midribs.

The magnification of each diagram was conveniently modified in each species in different degrees respectively and the length of the internodes was greatly shortened.

Fig. 1. *R. sceleratus* L.

Erect stem. The leaf trace strands of the Type A are three in number. At the lowest node a few strands of the Type B are recognized. The divergence is $2/5$.

Fig. 2. *R. Vernyi* FRANCH. et SAV. var. *japonicus* NAKAI

Erect stem. The strands of the Type A are also three in number. A large space at each node is the gap of the lateral shoot.

Fig. 3. *R. chinensis* BUNGE

Erect stem. The strands of the Type A are three to nine and variable in each node. They are reduced to three at the uppermost node. The divergence is almost $2/5$.

Fig. 4. *R. Zuccarini* MIQ.

Erect stem. A leaf trace consists always of three strands, only the midrib being of the Type A. Both trilacunar and unilacunar conditions are found in one and the same stem.

Fig. 5. *R. pygmaeus* WAHL.

Erect stem. Nodal condition is trilacunar and the strand of the Type A is also one in number, lateral two being of the Type B.

Fig. 6. *R. acris* L. var. *Steveni* REGEL

Erect stem. The leaf trace behaviour is similar to that of *R. Vernyi* (Fig. 2), but in this species all the strands are connected laterally at the node.

Fig. 7. *R. Kawakamii* MAKINO

Stolon. Only the midrib is of the Type A and the nodal condition is usually trilacunar. Lateral nerves of the leaf are often missing. The midrib is connected by the lateral strands at the node.

Fig. 8. *R. aquatilis* L. var. *flaccidus* MAXIM.

Submerse stem. General feature is similar to the former species.

Fig. 9. *R. flagellifolius* NAKAI

Three strands are supplied for a leaf also in this species. Lateral strands are often reduced, midrib being of the Type A. The leaf trace is, as a rule, unilacunar but often is trilacunar.

PLATE II

All the figures are microphotographs of the cross section made by the paraffin method.

Fig. 10. *R. japonicus* THUNB.

Vascular bundle of the erect stem. A bundle is entirely surrounded by a thick mechanical sheath, representing the bundle of the typical 'Ranunculus Type' of the writer. Xylem is V-shaped and both arms of the metaxylem consist of rather large vessels. A group of the cells with thin walls is phloem. ($\times 170$)

Fig. 11. *R. sceleratus* L.

Vascular bundle of the erect stem. A bundle is protected by a fibrous mass only on the phloem side (uppermost area of the photograph) without being entirely enclosed. An example of the bundle of the 'Anemone Type' of the writer. Great amounts of the secondary xylem-elements are observed. ($\times 25$)

Fig. 12. *R. sceleratus* L.

Same section as shown in Fig. 11, much more enlarged. Secondary xylem consists of vessels without containing any parenchymatous cells among them. ($\times 200$)

Fig. 13. *R. yatsugataensis* HONDA et KUMAZAWA

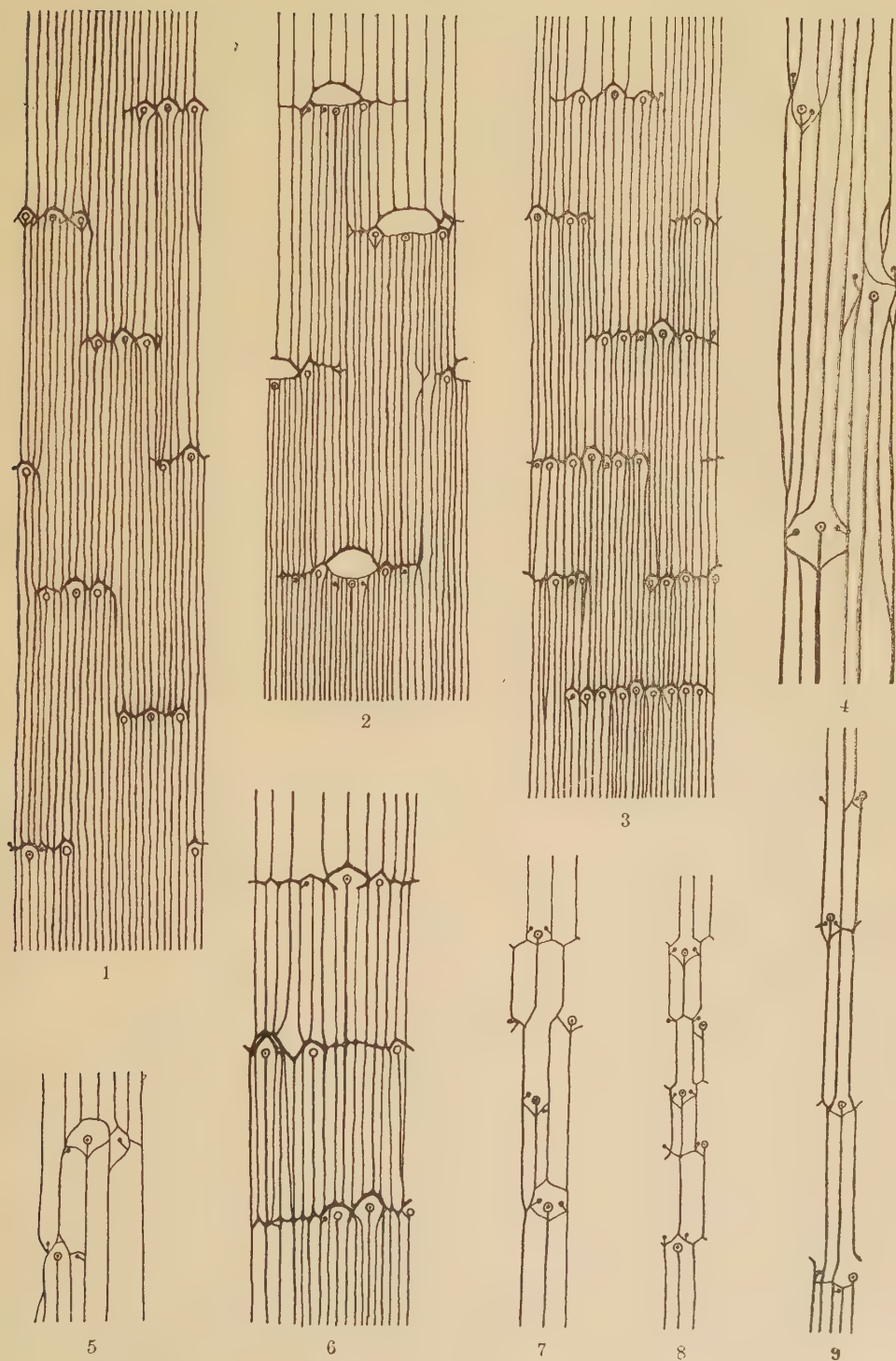
Vascular bundle of the upper part of the peduncle. The bundle is not protected by hardly any mechanical element and the xylem (lower half of the photograph) is not represented by the letter V, consisting of the small vessels and parenchymatous cells of rather uniform size. ($\times 260$)

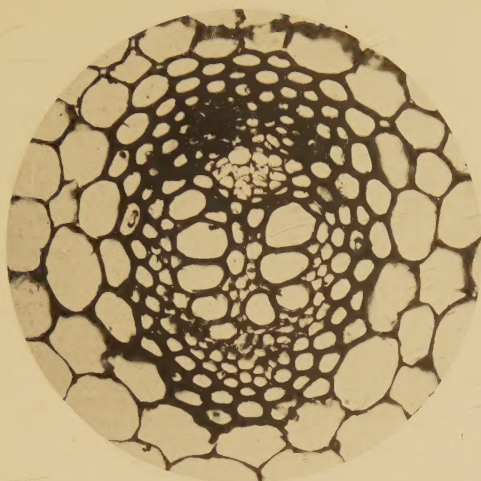
Fig. 14. *R. Vernyi* FRANCH. et SAV. var. *japonicus* NAKAI

Lower part of the floral receptacle in the older stage. Some amounts of the secondary vessels are now produced at the centre of the photograph, but the lignification of the walls occurs suddenly at the same time. Secondary phloem is seen at the upper part of the photograph. ($\times 170$)

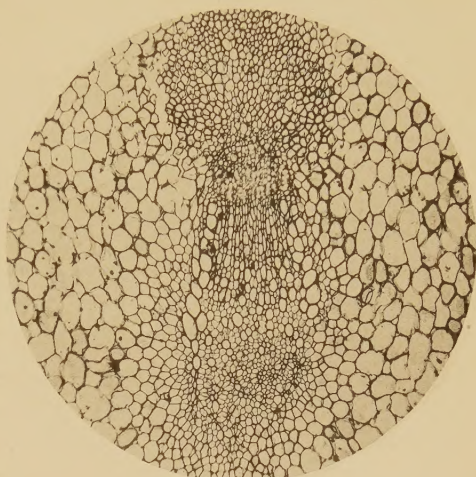
Fig. 15. *R. chinensis* BUNGE

Lower part of the floral receptacle in the older stage. Secondary elements are clearly produced, thus resulting in a vascular cylinder. There are some mechanical elements at the peripheral parts of the pith. ($\times 50$)

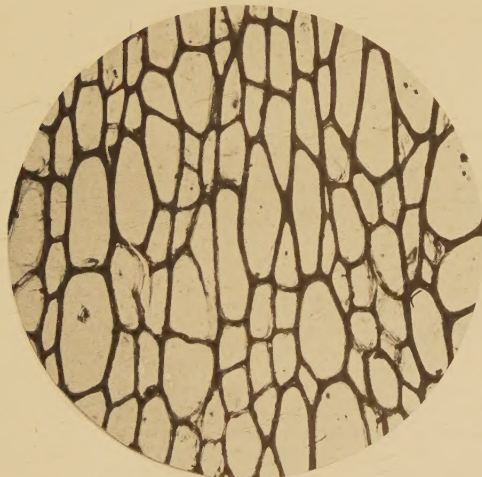




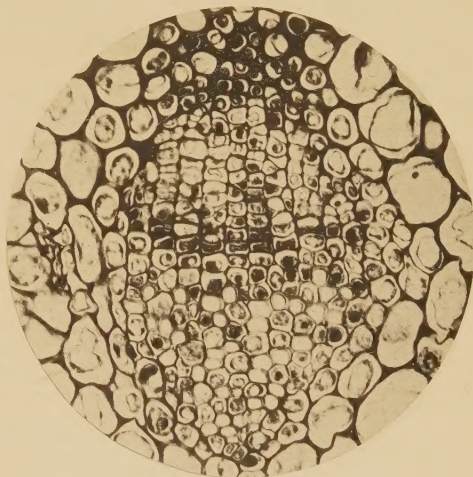
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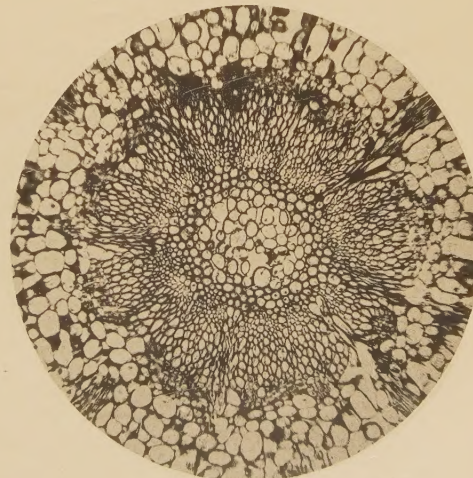
12



13



14



15

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CONTENTS

| | |
|---|-----|
| M. KUMAZAWA:—Studies on the Structure of Japanese Species of Ranunculus. | 297 |
|---|-----|

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